NOTES ON THE ECOLOGY OF FOUR SPECIES OF PYGOPODID LIZARDS IN THE GREAT VICTORIA DESERT

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ABSTRACT

Following a brief review of the literature on pygopodid lizards, ecological data are presented for *Delma butleri*, *Delma nasuta*, *Lialis burtonis*, and *Pygopus nigriceps*. *D. nasuta* and *D. butleri* are both diurnal and nocturnal, *L. burtonis* is crepuscular, and *P. nigriceps* is nocturnal. Active body temperatures were highest in *D. butleri* and lowest in *P. nigriceps*. Both *Delma* species climb inside spinifex tussocks, *L. burtonis* and *P. nigriceps* are terrestrial, but one *P. nigriceps* was found 0.2m above ground on top of a spinifex tussock. Most individuals of both species of *Delma* were found on desert flats. *Lialis burtonis* and *P. nigriceps* had broader habitat niche breadths and were associated with both flats and sand ridges. Tails are shortest in *L. burtonis* and *P. nigriceps*, and 3+ times snout-vent length in both *Delma* species. All these pygopodids are dietary specialists, although food niche breadths vary from 1.0 to 4.26. *Lialis burtonis* is most specialized, eating only lizards and largely skinks. Mating occurs during the Austral Spring, clutch sizes always consist of 2 eggs and relative clutch mass varied from 1.37 to 1.76 among species.

INTRODUCTION

Pygopodids are uncommon Australian lizards, sometimes called flap-foots due to their complete lack of fore limbs and greatly reduced vestigial hind limbs. Pygopodids, which have undergone an adaptive radiation, are a monophyletic family derived from Diplodactylid geckos (Kluge 1974, 1976; Jennings *et al.* 2003). These cryptic lizards are difficult to find and study and relatively little is known about most of the 40-odd described species. Six genera are recognized, two of which (*Ophidiocephalus* and *Pletholax*), are monotypic and scarcely known (but see Downes *et al.* 1997; Ehmann 1978, 1981, 1992;

and Bamford 1998). *Delma* (including the former "*Aclys*") is the most species-rich genus, with more than 20 named widespread species, which include both terrestrial and arboreal species. Some *Delma* can lift themselves completely off the ground using their long and powerful tails (Bauer 1986). Most "swim" rapidly through grass tussocks. The second largest genus *Aprasia* is also widespread, with 11 species, all of which are burrowers with relatively short tails (Parker 1956). *Aprasia* have converged on blind snakes, their diets consist of larvae and pupae of ants of several genera (Webb and Shine 1994). Food habits and reproductive biology of pygopodids were reviewed by Patchell and Shine (1986). *Pygopus* (including "*Paradelma*") includes 5 terrestrial nocturnal species that mimic venomous snakes. These lizards rear up their heads and feint menacingly, hissing and lunging like snakes, but give away their true identity when they flick out their short black blunt gekkonid tongue. One of the best studied species is *Lialis burtonis*, an ecological equivalent of a snake that sits and waits for large skinks and has hinged teeth like some skink-eating snakes (Savitzky 1981; Patchell and Shine 1986a, 1986b, 2009). As a further example of its convergence on snakes, caudal luring has been reported in *Lialis* (Murray *et al.* 1991). Moreover, *Lialis* has elliptical pupils and is crepuscular as are many snakes (Neill 1957). Evolutionary advantages of limblessness in pygopodids are discussed by Shine (1986).

METHODS

Over the last 42 years, from September 1966 through November 2008, on 11 separate research expeditions, I have spent 41 months and 1256 days in the field studying lizards, mostly during Austral Springs in the Great Victoria Desert (GVD) of Western Australia. However, a few specimens were captured outside the GVD. Up until 1979, all lizards were collected by hand, and data were obtained on date and time of activity, ambient air temperature, active body temperature, habitat and microhabitat. Data for 3 species of pygopodids were summarized in Pianka (1986), in which *D. butleri* was unfortunately misidentified as "*D. fraseri*." Beginning in 1989, most lizards were collected using pit traps (62,226 pit trap days), which provided more limited qualitatively different information.

Items within stomachs were sorted among 15 categories, mostly arthropod orders. Items were counted and volumes estimated to the nearest cubic millimetre for each category. Volumes were estimated by placing a one millimetre thick layer of material over square millimetre grid paper and approximating total volume. Each lizard's counted stomach contents were kept individually and stored in ethanol. Dietary niche breadths were estimated using the inverse of Simpson's index of diversity [$D = 1/ \Sigma p_i^{\,2}$] where p_i is the proportion by volume of food items in stomachs based on 15 prey categories.

All lizards were collected and deposited in the LA County Museum of Natural History and the Western Australian Museum. Here, I report augmented ecological information on 4 species of pygopodids: *Delma butleri* (N=101), *Delma nasuta* (N=15), *Lialis burtonis* (N=60), and *Pygopus nigriceps* (N=57).

RESULTS

Time of Activity

Most pygopodids were active during the warmer months of October through February. In the following, all times are decimalized in metric units. *Delma butleri* are active during the day (mean time of day = 10.02, N=12, range 7.5 to 12.42), but also in late afternoon and evening hours (mean time =18.76, N=6, range 16.62 to 20.58). Of the 15 *Delma nasuta* collected, one was active at 8.5 (0830) AM, 11 were captured or pit trapped during the night or in early AM, two were active during daylight hours and pit trapped during the afternoon, and one was found active at night. Three *Lialis* were active during morning hours (mean time 8.5, range 7.3 to 9.12) and 9 were active in the afternoon and evening (mean = 16.87, range 14.6 to 19.5), indicating crepuscular activity. All *Pygopus* were active at night (mean time = 19.72, N=16, range 19 to 21.57).

Temperature Relationships

In this study (Table 1), the diurnal *Delma butleri* had the highest active body temperatures ranging from 27.7 to 35.2°C, with a mean of 31.74°C. Air and body temperature was obtained for only one *D. nasuta* which was active at 8.5 (0830) AM (air =24.4 and body = 29.8°C). Average body temperature chosen by *Lialis* in a laboratory thermal gradient was 35.1°C (Bradshaw *et al.* 1980); higher body temperatures were selected after feeding and lower body temperatures when lizards were starved. Body temperatures of eleven wild-caught individual *Lialis* ranged from 23.2 to 37.7°C with a mean of 29.0°C. Active body temperatures of nocturnal *Pygopus* were lower, ranging from

Table 1. Ambient air temperatures and active body temperatures for 3 species with data, along with the slope of regressions of active body temperatures on ambient air temperatures (Sample sizes in parentheses).

Species	Air Temperature (N)	Body Temperature (N)	Slope
D. butleri	28.48 (16)	31.74 (8)	0.560
L. burtonis	25.9 (12)	29.0 (11)	0.789
P. nigriceps	24.42 (15)	24.88 (12)	0.762

20.8 to 28.2 (mean 24.88). Slopes of regressions of active body temperature on ambient air temperature were lower for *Delma butleri* an indication of thermoregulation (Huey and Slatkin 1976). Steeper slopes for *Lialis* and *Pygopus*, relative to *Delma*, suggest that they are thermoconformers.

Microhabitat and Habitat

Both species of *Delma* were strongly associated with spinifex grass (*Triodia basedowi*), through which they "swim" rapidly and with ease. All *Lialis* were terrestrial and were found in a variety of microhabitats. *Pygopus* are largely terrestrial although one individual was active 0.2 metres above ground on top of a spinifex tussock. Most *D. butleri* and *D. nasuta* were found on desert flats. *Lialis* and *Pygopus* were distributed more evenly across habitats, being associated with the flats as well as sandridges, and have broader habitat niche breadths (Table 2).

Size, Relative Tail Length

Pygopus and *Lialis* are large and have relatively short tails, whereas both species of *Delma* are smaller and have considerably longer tails, relative to their snout-vent lengths (Table 3).

Diets

All these pygopodids are dietary specialists, although food niche breadths calculated with Simpson's index of diversity (see above) vary from 1.0 to 4.26 (Table 4). *Lialis* is most specialized,

Table 2. Percentages of lizards found in various habitats (Sample sizes in parentheses). Lizards found at an interface between habitats are split between both. Habitat niche breadths calculated with the inverse of Simpson's index of diversity, $1/\Sigma p_i^2$ where p_i represents the proportion of animals in habitat i.

Species	**Flat**	**Base**	**Slope**	**Crest**	**Total**	**Habitat NB**
D. butleri	84.2 (85)	14.9 (15)	0.5 (0.5)	0.5 (0.5)	101	1.37
D. nasuta	66.7 (10)	13.3 (2)	6.7 (1)	13.3 (2)	15	2.06
L. burtonis	35.0 (21)	29.2 (17.5)	15.8 (9.5)	20.0(12)	60	3.67
P. nigriceps	31.6 (18)	36.8 (21)	7.9 (4.5)	23.7 (13.5)	57	3.36

Table 3. Average snout-vent length (SVL) and tail lengths (in mm), ratio of tail length over SVL, and mean body weight (in grams).

Species	**Snout-Vent Length (N)**	**Tail Length (N)**	**Tail/SVL (N)**	**Weight (N)**
D. butleri	67.9 (99)	200.1 (58)	3.10 (58)	3.34 (98)
D. nasuta	86.9 (15)	261.3 (7)	3.19 (7)	6.45 (15)
L. burtonis	156 (44)	186 (23)	1.27 (23)	9.89 (42)
P. nigriceps	160 (58)	217 (27)	1.42 (27)	13.46 (58)

Table 4. Proportions of 15 different prey categories by volume in pygopodid stomachs.

Species/Prey Type	*D. butleri*	*D. nasuta*	*Lialis*	*Pygopus*
Centipedes	0.0435	0	0	0
Spiders	0.3897	0.0787	0	0.2681
Scorpions	0	0	0	0.2691
Ants	0.0035	0	0	0.0165
Orthopterans	0.2609	0.7191	0	0.1094
Thysanura	0.0486	0.0224	0	0
Blattaria	0.0400	0	0	0
Phasmids/Mantids	0.0052	0	0	0
Isoptera	0.0626	0.0337	0	0.0202
Diptera	0.0209	0	0	0.0101
Larvae	0.0453	0	0	0
Other Insects	0.0261	0.1011	0	0
Vertebrates	0	0	1.0	0
UnIdentified	0.0208	0	0	0.2965
Other	0	0.0449	0	0.0101
Total Volume of Prey, cc.	5.75	0.89	10.75	5.94
Dietary Niche Breadth	4.26	1.86	1.0	3.94
Number of Stomachs	85	14	44	49
Percentage of Empty Stomachs	29.1	35.7	79.5	36.7

eating only other lizards, largely skinks (80% of stomachs were empty). Species of skinks found in *Lialis* stomachs include *Lerista bipes, Menetia greyi, Ctenotus dux,* and *Ctenotus quattuordecimlineatus. Pygopus* eat predominantly spiders and scorpions, which they capture when these arthropods are active above ground at night. *Delma butleri* consume spiders and orthopterans, and *Delma nasuta* prey mainly on orthopterans.

Reproduction

In all 4 species, testes were enlarged in September, October and November suggesting that mating takes place during the Austral Spring. Two *Delma butleri* females each contained 2 eggs in their oviducts, clutch volume as a fraction of female body weight (relative clutch mass, RCM) were 0.132 and 0.160 (mean 0.146). Four *Lialis* females each had 2 eggs in their oviducts, clutch volumes as a fraction of body weight for these females were 0.114, 0.130, 0.150 and 0.153 (mean RCM 0.137). Two *Pygopus nigriceps* females each had 2 eggs in their oviducts, with relative clutch masses of 0.116 and 0.235 (mean RCM 0.176).

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